CHROMOSOME NUMBERS OF SOME NORTH AMERICAN SPECIES OF ASTRAGALUS (LEGUMINOSAE)

G. F. LEDINGHAM and M. D. FAHSELT

University of Saskatchewan, Regina Campus, Regina, Saskatchewan

Astragalus, with nearly two thousand species, is one of the largest genera of the flowering plants. It is widespread in both Old and New World but it is most abundant in the northern hemisphere. In the Old World, where there are some 1,600 species, the greatest number of taxa occur in southwest Asia with gradual decrease westward around the Mediterranean in both Europe and Africa and north and east through Asia to the Bering Strait. In the New World there are some 300 species concentrated in the western United States with a few extending into Mexico or into Canada and Alaska. There are no species in tropical America but there are about ninety species in the high western parts of South America.

Ledingham (1960) speculates that *Astragalus* is at least biphyletic since New and Old World species have different chromosome numbers. Old World species have a basic haploid chromosome number of eight (Senn, 1938; Darlington and Wylie, 1955, Löve and Löve, 1961) and show a high percentage of polyploidy. New World species have haploid chromosome numbers of 11, 12 or 13 (Vilkomerson, 1943; Head, 1957; Turner, 1956) and show less than one per cent of polyploidy. The nine South American species of *Astragalus* so far counted have either 11 or 13 as gametophyte chromosome number (Ledingham, 1960) so they seem to be a part of the New World phylogenetic line.

Since some species of *Astragalus* and *Oxytropis* are circumpolar, occurring in both New and Old World (Yurtsev, 1963), it would seem that the geographic barrier in the Bering Strait region is relatively recent. The circumpolar species are all 8-chromosome species or polyploids of these so evidently it was the Old World group which was able to use the migration route and invade the New World. There are no known cases of 11- or 12-chromosome species which have spread into the Old World. The decreasing abundance of 8-chromosome species as one moves from Alaska south and east supports the idea that a number of Old World species entered the New World by this route. Some of these naturally spread farther than others.

The North and South American species of *Astragalus* are now separated by a wide tropical zone which acts as an effective geographic barrier. The species are closely related but none of them occurs in both regions (Johnston, 1947). The absence of common species would indicate that the barrier has been present relatively longer than the barrier in

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the Bering Strait region, giving time for the evolution of different forms. The fact that there still is considerable morphological and chromosome number similarity would indicate that *Astragalus* species in North and South America, though separated for a considerable length of time, are actually a part of the same phylogenetic line and they are more closely related than New World species are to the 8-chromosome Old World species.

Since Old World species of *Astragalus* and *Oxytropis*, including a few which have spread recently into northern North America, have consistently 8 chromosomes or some multiple of 8, and since New World species have n=11, 12 or 13, they must be two different phylogenetic lines (Ledingham and Rever, 1963). If the divergence occurred after the origin of the genus then we may still find some species with chromosome numbers which will explain how the evolution took place. If the divergence occurred before the evolution of the ancestral *Astragalus* then the explanation of the relationship may be found in other genera of the Leguminosae. Turner and Fearing (1959) suggest that there was a split in the Caesalpinoideae giving evolutionary lines with higher or lower chromosome numbers and that these provided two origins for species and genera of the Papilionoideae. If this theory proves tenable then the Papilionoideae, and *Astragalus* in particular, provide a remarkable example of parallel evolution, and the origin of the divergence of the two phylogenetic lines of *Astragalus* would have to be sought in the Caesalpinoideae. This hypothesis seems improbable.

Ledingham (1960), finding that *Astragalus somalensis* Taub. ex Harms had the intermediate chromosome number 2n=20, thought that the phylogenetic split must have occurred early in the evolution of the genus and he hoped to find other species with intermediate chromosome number. Since our plants of *A. somalensis* winterkilled without giving flowering or fruiting material we germinated more seeds. The material had been obtained from the Grassland Research Station, Kitale, Kenya, East Africa. The count 2n=20 was confirmed (Ledingham and Rever, 1963) and the voucher plants were watched as they grew. The leaflets were conspicuously veiny and the arrangement of the leaflets in the bud was not like other *Astragalus* species we had seen. We were not surprised when Gillett (1963) revised this species, along with two others from East Africa, and placed them in the genus *Galega*.

This paper reports 69 counts on 49 species including 28 species and 6 varieties not previously reported. There are now over 310 species of *Astragalus* counted. The additional counts reported here emphasize again that the chromosome number in this complex of species is stable and further support the contention that New and Old World species of *Astragalus* belong in different phylogenetic lines.

MATERIALS AND METHODS

The species reported in this paper, except for five Old World species which came as seed from botanical gardens, were collected in their native habitats by people interested in the Leguminosae. The specimens, most of which are available in the University of Saskatchewan, Regina Campus herbarium, have in many cases been identified by Mr. R. C. Barneby, New York Botanical Garden. Mature seeds were removed and germinated in petri dishes to give root tips for chromosome counts. Some seeds have also been germinated to give additional study material and voucher specimens. Since these species are mostly slow growing perennials, flowering and fruiting vouchers are not yet available from our cultivated stocks. The root tips used for chromosome counts were pretreated with 8-hydroxyquinoline before fixation and staining. The standard procedure for the Feulgen stain was used in making the root tips squashes.

RESULTS

Chromosome counts for species of *Astragalus* and *Oxytropis* studied here during the summer of 1963 are presented in Tables I and II. Table I reports somatic chromosome numbers (22, 24 and in two cases 26) and collection data for 39 collections representing 28 species of New World *Astragalus*. Table II reports somatic chromosome numbers (16, 32, 48 and 42) for 30 collections (15 of which were made in North America) of 21 Old World species of *Astragalus* and *Oxytropis*.

The typical New World species of *Astragalus* listed in Table I were collected in their natural habitats in the western parts of United States, except for one species which was collected in Canada. There are voucher herbarium specimens, mostly in the herbarium of the University of Saskatchewan, Regina Campus, for each of the collections. One collection. *A. coccineus*, is represented only by fruits and a single dried flower, but the long crimson petals provide convincing evidence of the identity of the species. Some of the collections were badly parasitized and contained only a few viable seeds so that a sufficient number of good counts could not always be made; the chromosome number is reported in four cases with some reservation. Examination of Fig. 12, *A. calycosus*, 2n=22, shows that it is not easy to be sure whether the count is 2n=22 or 24. A quick count of this group may give 24, for there is a conspicuous nonstaining area, eg. lowest chromosome on the left, in one pair of chromosomes. Other cells in this same slide may, however, look more like Fig. 5 which is a typical chromosome group from *A. johannis-howellii*. Fig. 9, *A. whitneyi*, 2n=22, also shows this appearance of an extra pair of small chromosomes which may lead to some disagreement between counts of New World species of *Astragalus*.

Three species counts of 2n=24 confirm previous counts. *A. kentrophyta*, 2n=24 was reported by Ledingham (1960), but that report gives the wrong author for the species. *A. preussii*, 2n=24, was reported in 1943 by Vilkomerson. The earlier reports on these two species did not identify the variety counted. *A. spatulalus*, 2n=24, was reported by Ledingham (1957).

TABLE I. SOMATIC CHROMOSOME COUNTS FOR NEW WORLD ASTRAGALI

Species	Seed no.	Collection no.	Origin	2n chr. no.	Fig.
A. amphioxys Gray					
var. *amphioxys*	6424	Rever 72	Arches Nat. Monument, Utah	22	2
"	6439	Rever 67	Crystal Geyser, Utah	22	
A. *argophyllus* Nutt.					
var. *martini* Jones	6430	Rever 54	Castlegate, Utah	22 ?	
A. *calycosus* Torr.	6402	DeDecker 1522	White Mts. California	22	12
A. *ceramicus* Sheld.					
var. *ceramicus* Sheld.	6304	Barneby 13,121	Escalante, Utah	22	
var. *imperfectus* Sheld.	6455	Porter 3954	Gillette, Wyoming	22	7
A. coccineus Bdg.	6386	DeDecker 22/7/62	Inyo Mts., California	22	6
A. cymboides Jones	6429	Rever 58	Wellington, Utah	24	10
"	6453	Rever 83	Huntington, Utah	24	
A. desperatus Jones					
var. *desperatus* Jones	6418	Rever 78	Moab, Utah	24	1
"	6423	Rever 71	Arches Nat. Monument, Utah	24	
A. eastwoodae Jones	6299	Barneby 13,064	Gypsum Gap, Colorado	26	
A. flavus Nutt.					
var. *flavus*	6416	Rever 81	Moab, Utah	26	

A. *inyoensis* Sheld.	6403	DeDecker 1519	Inyo Mts., California	22	3
A. *johannis-howellii* Barn.	6404	DeDecker 1505	Crowley Lake, California	22	5
*A. *kentrophyta* Gray var. *coloradensis* Jones	6308	Barneby 13,115	Glen Canyon City, Utah	24	
*A. *lentiginosus* Dougl.					
var. *palans* Jones	6425	Rever 73	Arches Nat. Monument, Utah	22	
var. *palans* Jones	6427	Rever 76	Moab, Utah	22	
var. *fremontii* (Gray) Wats.	6387	DeDecker 1484	Santa Rita Flat, California	22	4
A. *miguelensis* Greene	6507	Raven 18,012	San Clemente Island, California	22	11
*A. *miser* Dougl. var. *serotinus* (Gray) Barn.	6499	Turner 11,180	Pocahontas, Alberta	22	
*A. *mollissimus* Torr. var. *thompsonae* (Wats.) Barn.	6417	Rever 80	Moab, Utah	22	
”	6426	Rever 75	Devil's Garden, Utah	22	
*A. *nuttallianus* DC. var. *micranthiformis* Barn.	6302	Barneby 13,110	Coconino Co., Arizona	24	
A. *oophorus* Wats.	6390	DeDecker 488	Badger Flat, California	24	
A. *plattensis* Nutt.	6289	Porter 8385	Cook Co., Wyoming	22 ?	

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* These species counted previously; details in text.

*A. *preussii* Gray					
var. *preussii*	6419	Rever 66	Green River, Utah	24	
”	6428	Rever 79	Moab, Utah	24	
*A. *purshii* Dougl. var.					
glareosus (Dougl.) Barn.	6414	Rever 111	Boise, Idaho	22	8
”	6440	Rever 112	Boise, Idaho	22	
lectulus Jones	6406	DeDecker 1,525	Coyote Ridge, California	22	
longilobus Jones	6393	DeDecker 1,472	Harkless Flat, California	22	
A. *ravenii* Barn.	6394	DeDecker 1,112	Sawmill Pass, California	24	
A. *serenoi* (Kuntze) Sheld.	6389	DeDecker 1,469	Harkless Flat, California	24 ?	
A. *shortianus* Nutt.	6285	Porter 8,460	Albany Co., Wyoming	24 ?	
*A. *spatulatus* Sheld.	6307	Barneby 13,234	Biddle, Montana	24	
A. *utahensis* (Torr.) T.&G.	6457	Rever 35	Pocatello, Idaho	22	
A. *whitneyi* Gray	6407	DeDecker 1,535	Coyote Flat, California	22	9
A. *zionis* Jones	6298	Barneby 13,111	Coconino Co., Arizona	22	

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* These species counted previously; details in text.

The previous report of chromosome number of *A. miser* var. *serotinus* gives 2n=24 (Ledingham, 1958). Since our 1963 study shows 2n=22, we suspect that our original report is in error. Ledingham (1960) reported 2n=22 for *A. nuttallianus* var. *nuttallianus* but the present study shows 2n=24 for var. *micranthiformis*. The varieties of *A. nuttallianus* are both quick growing annuals and it is possible that both counts are correct.

In *Astragalus lentiginosus* there have been previous reports of 2n=22 reported for var. *palans* (Vilkomerson, 1943), var. *lentiginosus* (Head, 1957) and var. *variabilis* (Ledingham, 1960). This paper confirms the previous count of var. *palans* (two collections) and reports 2n=22 for var. *fremontii*.

In *A. purshii*, Head (1957) reported counts of 2n=22 for var. *purshii* and var. *glareosus*. This paper confirms the count for var. *glareosus* and reports 2n=22 for var. *lectulus* and var. *longilobus*. The chromosome number seems stable for the many varieties of the highly variable species *A. purshii* and *lentiginosus*.

The remaining species, for which there was a previous chromosome count, is *A. mollissimus*. The present report for var. *thompsonae* agrees with Ledingham's (1960) report for var. *earlei*. Previously Head (1957) had reported 2n=24 for var. *earlei*.

No attempt was made to obtain Old World material for the 1963 studies but some seed samples did become available and routine chromosome counts were made. These counts are reported in Table II even though voucher specimens are not available for every collection. Each of these Old World species, except one, obviously belongs to an 8-chromosome series in which diploids are common but tetraploids and hexaploids frequently occur. Different chromosome numbers may be present in the same species. Table II includes some species of Old World *Astragalus* and *Oxytropis* which have migrated into northwestern North America. It should be pointed out that eleven of the fifteen North American collections reported in Table II were made in Canada or Alaska whereas in Table I only one of the 39 collections was made north of the Canada-U.S.A. border.

The chromosome numbers of 13 of the 21 taxa listed in Table II have been reported before. In all cases except two the present report agrees with previous reports and details need not be given again here. *Astragalus odoratus* was previously reported as having 2n=64 by Ledingham (1960). When this material was finally grown out it proved to be *A. cicer*. The seed packet had been wrongly identified and Ledingham had made his report before verifying the identity of his material. *A hamosus* is reported (Darlington and Wylie, 1955) as having 2n=48. We are convinced that this number is not correct but we found these chromosomes very difficult to separate and count and give a tentative count of 2n=ca 42.

Table II gives chromosome counts of four samples of *A. alpinus*, two identified as var. *brunetianus*. The collection from Churchill, Manitoba

TABLE II. SOMATIC CHROMOSOME COUNTS FOR OLD WORLD ASTRAGALI

Species	Seed no.	Collection no.	Origin	2n chr. no.	Fig.
**A. alpinus L.*	6230	cultivated	Acad. Science, Leningrad	16	
"	6243b	E. Beckett	Churchill, Manitoba	32	
var. *brunetianus* Fern.	6399	A. Dechamplain 2/7/58	Rimouski, Quebec	16	
"	6400	Dutilly & Lepage 30/7/58	Missinaibi, Ontario	16	
A. angustifolius Lam.	6442	O. Tosun	Ankara, Turkey via USDA.	32	16
**A. eucosmus* Robins	6396	J. G. Dickson 11/8/56	Big Delta, Alaska	32	
**A. hamosus* L.	6002	V. Tackholm	Egypt	ca 42	
"	6273	N. Feinbrun	Peleponese, Greece	ca 42	
" (as *A. Bucesas*)	6438	cultivated	Madrid Botanical Garden	ca 42	18
A. hololeios Bornum	6493	cultivated 4309	Universitatis Bergensis, Norway	16	19
A. micropteris Fisch.	6446	O. Tosun	Ankara, Turkey via USDA.	32	14
**A. monspessulanus* L.	6361	E. Müller 22/8/61	Tiefenkastel, Switzerland	16	
**A. odoratus* Lam.	6445	O. Tosun	Ankara, Turkey via USDA.	16	13
A. ovalis Boiss.	6443	O. Tosun	Ankara, Turkey via USDA.	16	17

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* These species previously counted; cases of disagreement discussed in the text.

**A*. sesameus* L.	6505	cultivated	Madrid Botanical Garden	16	
A. spinosus Muschl	6436	J. Mandaville 20/4/63	Saudi Arabia	16	15
**A*. uliginosus* L.	6160	cultivated	Vladivostok, USSR.	16	
**A*. umbellatus* Bunge	6397	J. G. Dickson 26/8/56	Glenn Highway, Alaska	16	
**A*. vulpinus* Willd.	6503	cultivated	Russia	16	20
**Oxytropis campestris* (L.) DC					
var. *gracilis* (A. Nels.) Barn.	6500	G. H. Turner 15/8/60	Fort Saskatchewan, Alberta	32	
**O*. deflexa* (Pall.) DC.	6502	cultivated	Udaipur, India	16	
var. *sericea* T. & G.	6496	G. H. Turner 24/7/60	Fort Saskatchewan, Alberta	16	
"	6497	G. H. Turner 10/8/60	Fort Saskatchewan, Alberta	16	
**O*. halleri* Bunge	6384	cultivated	Inst. Alpin du Lautatet, France	16	
O. monticola A. Gray	6506	cultivated	Kamploops Expt. Farm, B.C.	48	22
O. multiceps Nutt.	6286	C. L. Porter 8322	Albany Co., Wyoming	16	
O. parryi Gray	6408	M. DeDecker 1523	Mono Co., California	16	21
"	6409	M. DeDecker 1534	Inyo Co., California	16	
**O*. sericea* Nutt.	6288	C. L. Porter 8458	Albany Co., Wyoming	48	
var. *spicata* (Hook.) Barn.	6498	G. H. Turner 11071	Jasper Nat. Park, Alberta	48	

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* These species previously counted; cases of disagreement discussed in the text.

has 2n=32 while the collections from Ontario, Quebec and Russia have 2n=16. Professor C. Favarger in personal conversation at the IXth International Botanical Congress in Montreal in 1959 said that he had found both 2n=16 and 2n=32 in some Switzerland collections of *A. alpinus.* Ledingham (1960) reported on four collections, three from Alberta, Manitoba and Saskatchewan having 2n=16 and one from Yukon having 2n=32. The count of 2n=ca 56 listed in Darlington and Wylie (1955) is considered erroneous.

It should be pointed out that although the present chromosome count 2n=32 for *O. campestris* var. *gracilis* agrees with some of the previous reports for this species there are also reports of 2n=48. Ledingham (1957, 1960) reports 2n=32 for six Saskatchewan and one Alberta collection. Jalas (1950) for ssp. *sordida* and Ledingham (1960) for one Old World and Ontario and British Columbia material report 2n=48.

Plates I and II give some camera lucida drawings of chromosomes of representative species of New World and Old World *Astragalus.* These drawings are all done with the same apparatus and at the same magnification. Although it seemed as if New World species had smaller chromosomes which were more difficult to separate and count this is not supported by the drawings. Plate I illustrates chromosomes of New World species and Plate II shows chromosomes of Old World species of *Astragalus.*

DISCUSSION

This paper reports chromosome counts for 28 species of *Astragalus* not previously reported. Twently of these counts are of New World species (Table I and Figs. 1-12) and they form an aneuploid series with n=11, 12, or 13. Eight new counts are reported for Old World species, 5 in *Astragalus* and 3 in *Oxytropis,* (Table II and Figs. 13-22) and these have 2n=16, 32 or 48, i.e. are diploids, tetraploids or hexaploids of the 8-series.

These 28 counts together with additional counts for 21 other species for which there have been previous reports further support the conclusion (Ledingham, 1960) that there are two main phylogenetic lines in *Astragalus.* There are now counts for 109 New World species and all have n=11 (53 species), 12 (38), 13 (14), 14 (3) or 22 (*A. grayi,* the only New World tetraploid). There are counts for 202 Old World species of *Astragalus* and *Oxytropis* and they have n=8 (146 species), 16 (21), 24 (18), 32 (8), 40 (1), 48 (2), ca 80 (1) and others (5).

In an earlier paper Ledingham (1960) gave a count of n=10 for *Astragalus somalensis* and suggested that species with the intermediate chromosome numbers n=9 and 10 might form part of the aneuploid series which includes both Old and New World *Astragalus.* No further evidence has been found to support this idea, and since Gillett (1963) has removed *A. somalensis* to *Galega,* it seems less likely. There are now no known species with n=9 or 10 in the *Astragalus* complex.

The suggestion has been made (Turner, 1959) that the n=14, 13, 12 and 11 of New World species of *Astragalus* are derived hypoploids from an ancestral n=16 tetraploid species. There are, however, no tetraploids in North America except for a few circumpolar species which are actually a part of the Old World phylogenetic line. There are several species in the Old World which may be hypoploids, e.g. the annual conspicuously self-fertile species *A. boeticus,* 2n=30.

Our counts of 2n=ca 42 for *A. hamosus* make us suspicious of the previous report of 2n=48 for this species. Our suggestion for the moment is that *A. hamosus* does not really belong in *Astragalus.* It seems likely that *A. hamosus* is a hexaploid in some n=7 phylogenetic line. Tetraploids in this line may include *A. pentaglottis,* 2n=28 (Senn, 1938; Ledingham, 1960) and *A. bubaloceras,* n=ca. 14-15 (Senn, 1938). Diploids of this n=7 line are unknown. There is, then, little evidence of hypoploids in Old World *Astragalus* and it seems very unlikely that New World *Astragalus* has arisen by chromosome loss from tetraploid (2n=32) plants of the Old World line.

Although we do not yet have enough information to reconstruct the evolutionary history of the Leguminosae, or more specifically of *Astragalus* and *Oxytropis,* it is clear that chromosome numbers can be used with considerable confidence to show true relationship in this family. This paper further establishes that New World and Old World species of *Astragalus* have had a different evolutionary history and must be considered as different subgenera or genera if taxonomy is to reflect true relationships. The chromosome evidence would indicate that *Oxytropis* is closely related to, or is a part of, the Old World *Astragalus.* It is now clearly established that chromosome number can be used as a significant character in this family. The relationships of species with anomalous counts should be studied critically.

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PLATE I

Figs. 1-12—Somatic chromosomes of New World species of *Astragalus* drawn with the aid of a camera lucida originally at x 2250 reduced by 50% in reproduction.

Fig. 1 *A. desperatus* var. *desperatus*, 2n=24, Rever 78.

Fig. 2. *A. amphioxys* var. *amphioxys*, 2n=22, Rever 72.

Fig. 3. *A. inyoensis*, 2n=22, DeDecker 1519.

Fig. 4. *A. lentiginosus* var. *fremontii*, 2n=22, DeDecker, 1484.

Fig. 5. *A. johannis-howellii*, 2n=22, DeDecker, 1505.

Fig. 6. *A. coccineus*, 2n=22, DeDecker, July 22, 1962.

Fig. 7. *A. ceramicus* var. *imperfectus*, 2n= 22, Porter 3954.

Fig. 8. *A. purshii* var. *glareosus*, 2n=22, Rever 111.

Fig. 9. *A. whitneyi*, 2n=22, DeDecker 1535.

Fig. 10. *A. cymboides*, 2n=24, Rever 58.

Fig. 11. *A. miguelensis*, 2n=22, Raven 18012.

Fig. 12 *A. calycosus*, 2n=22, DeDecker 1522.

Origin of material given in Table I.

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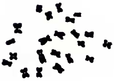

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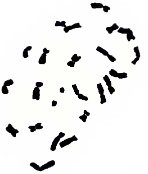

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11

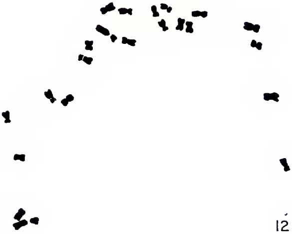

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PLATE II

Figs. 13-22. Somatic chromosomes of Old World species of *Astragalus* and *Oxytropis* drawn with the aid of a camera lucida originally at x 2250 reduced by 50% in reproduction.

Fig. 13. *A. odoratus*, 2n=16, O. Tosun.

Fig. 14. *A. micropteris*, 2n=32, O. Tosun.

Fig. 15. *A. spinosus*, 2n=16, J. P. Mandaville, April 20, 1963.

Fig. 16. *A. angustifolius*, 2n=32, O. Tosun.

Fig. 17. *A. ovalis*, 2n=16, O. Tosun.

Fig. 18. *A. hamosus*, 2n=ca. 42, Ledingham 2805.

Fig. 19. *A. hololeios*, 2n=16, Universitatis Bergensis 4309.

Fig. 20. *A. vulpinus*, 2n=16, Russia.

Fig. 21. *O. parryi*, 2n=16, DeDecker 1523.

Fig. 22. *O. monticola*, 2n=48, Kamloops 1939.


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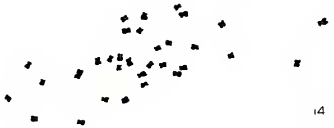
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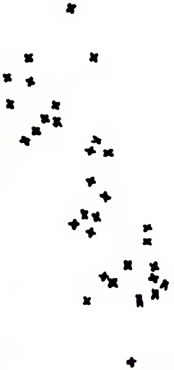
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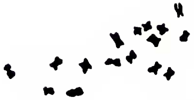
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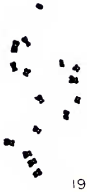
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